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## Bathymetric limits of chondrichthyans in the deep sea: A re-evaluation

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## ABSTRACT

Chondrichthyans are largely absent in abyssal (> 3000 m) habitats in most regions of the world ocean and are uncommon below 2000 m. The deeper-living chondrichthyans include certain rajids, squaliforms and holocephalans. Several hypotheses have been erected to explain the absence of chondrichthyans from the abyss. These are mostly based on energetics: deep-sea food webs are impoverished due to their distance from primary production, and chondrichthyans, occupying the highest trophic levels, cannot be supported due to entropy among trophic levels. We examined this hypothesis by comparing trophic levels, calculated from dietary data, of deep-sea chondrichthyans with those of deep-sea teleosts. Chondrichthyans were mostly above trophic level 4, whereas all the teleosts examined were below that level. Both small and medium squaloids, as well as sharks and skates of large size, feed on fishes, cephalopods and scavenged prey, and thus occupy the highest trophic levels in bathydemersal fish communities. In addition, whereas teleosts and chondrichthyans both store lipids in their livers to support long periods of fasting, chondrichthyans must devote much of their liver lipids to maintain neutral buoyancy. Consequently teleosts with swim bladders are better adapted to survive in the abyss where food sources are sparse and unpredictable. The potential prey field for both chondrichthyans and teleosts declines in biomass and diversity with depth, but teleosts have more flexibility in their feeding mechanisms and food habits, and occupy abyssal trophic guilds for which chondrichthyans are ill adapted.

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## 1. Introduction

Chondrichthyans are largely absent in abyssal (> 3000 m) habitats in most regions of the world ocean, and are uncommon below 2000 m (Musick, 2003; Priede et al., 2006), whereas many teleosts are resident below 3000 m and may occur at least as deep as 8370 m (Priede et al., 2006; Nielsen, 1977). Priede et al. (2006) examined several possible hypotheses that might provide a universal mechanism to explain chondrichthyan depth limitations. The most plausible of these was the absence of a swim bladder in chondrichthyans and its presence in large benthopelagic teleosts. They suggested that a swim bladder might confer an energetic advantage to teleosts in abyssal ecosystems, which are severely energetically limited (Gage and Tyler, 1991).

Laxson et al. (2009) offered an alternative hypothesis, and provided evidence to show that the ratio of urea/trimethylamine N-oxide (TMAO) declines linearly by four fold with depth in chondrichthyans on the continental slope, and may plateau at

about 3000 m. High levels of urea are maintained by chondrichthyans to maintain osmotic balance with seawater (Smith, 1931), and TMAO acts to stabilize the protein perturbing nature of the urea (Yancey, 2005). In addition, TMAO counteracts protein destabilization resulting from increasing hydrostatic pressure with depth in both chondrichthyans and teleosts (Laxson et al., 2009). Laxson et al. (2009) suggested that since TMAO may not be synthesized by chondrichthyans, but must be obtained through their food, they may not be able to accumulate sufficient TMAO to maintain osmotic balance and/or counter-balance the effects of pressure at great depths because of dietary limitation. Alternatively, chondrichthyans might be unable to drive urea accumulation to zero (thus allowing TMAO to increase) without becoming hyperosmotic to seawater, or TMAO may be toxic at concentrations above ~300 mmol. These hypotheses remain to be tested and will not be discussed further here.

Both Priede et al.'s (2006) and Laxson et al.'s (2009) principal hypotheses are predicated on differences between teleosts and chondrichthyans relative to food limitations in the deep sea. In the present paper we further examine differences between bathyal chondrichthyans and abyssal teleosts to evaluate the factors that

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might be limiting the former from the abyss. Our analysis includes examinations of: (a) trophic position, (b) ecological limitations, and (c) additional morphological/physiological limitations.

Because our hypothesis was that bathyal (1000–3000 m) chondrichthyans occupy higher trophic levels than bathyal and abyssal (> 3000 m) teleosts we chose teleosts for comparison that were large in size, and documented to be upper level predators or scavengers.

## 2. Materials and methods

Shark trophic levels (TLs) were taken directly from Cortes (1999) and skate TLs were taken directly from Ebert and Bizzarro

**Table 1**  
Prey categories used to calculate trophic levels of fishes (from Cortés, 1999).

Code	Species group	Trophic level
FISH	Teleost fishes	3.24
CEPH	Cephalopods (squids, octopuses)	3.2
MOL	Molluscs (excluding cephalopods)	2.1
CR	Decapod crustaceans (shrimps, crabs, prawns, lobsters)	2.52
INV	Other invertebrates (all invertebrates except molluscs, crustaceans, and zooplankton)	2.5
ZOO	Zooplankton	2.2
BIR	Seabirds	3.87
REP	Marine reptiles (sea turtles and sea snakes)	2.4
MAM	Marine mammals (cetaceans, pinnipeds, mustelids)	4.02
CHON	Chondrichthyan fishes (sharks, skates, rays, and chimaerids)	3.65
PL	Plants (marine plants and algae)	1

**Table 2**  
Mean trophic levels (TLs) of bathyal and abyssal teleost and chondrichthyan fishes, indicating which trophic index was used to calculate TL, as well as diet data sources. Neither Cortés (1999) nor Ebert and Bizzarro (2007) reported which trophic index was used to calculate shark or skate TL's (respectively). These values are denoted by "NR" and the number of studies used to calculate TL is indicated in parentheses.

Grouping	Species	Trophic level	# Stomachs examined	Trophic index	Source
<b>Synphobranchiids</b>					
<i>Anguilliformes</i>					
Synphobranchiidae	<i>Histiobranchus bathybius</i>	3.67	62	(%N+%W)/2	Martin and Christiansen (1997)
	<i>Synphobranchus brevidorsalis</i>	3.92	10	%IRI	Crabtree (1984)
	<i>S. kaupi</i>	3.94	177	(%N+%W)/2	Sedberry and Musick (1978)
	Group mean	3.84			
<b>Ophidiids</b>					
<i>Ophidiiformes</i>					
Ophidiidae	<i>Bassozetus normalis</i>	3.38	62	(%N+%W)/2	Crabtree et al. (1991)
	<i>B. taenia</i>	3.38	14	(%N+%W)/2	Crabtree et al. (1991)
	<i>Bathyonus pectoralis</i>	3.21	112	(%N+%W)/2	Crabtree et al. (1991)
	<i>Spectrunculus grandis</i>	3.47	9	%N	Mauchline and Gordon (1984b)
	Group mean	3.36			
<b>Large gadoids</b>					
<i>Gadiformes</i>					
Macrouridae	<i>Coryphaenoides armatus</i>	3.44	5	(%N+%V)/2	Sedberry (1975)
	<i>C. armatus (adults only)</i>	3.73	25	%F	Haedrich and Henderson (1974)
	<i>C. armatus</i>	3.80	282	%F+%W/2	Pearcy and Ambler (1974)
	<i>C. filifer</i>	3.92	59	%F+%W/2	Pearcy and Ambler (1974)
	<i>C. leptolepis</i>	3.36	80	%F+%W/2	Pearcy and Ambler (1974)
Moridae	<i>Antimora rostrata</i>	3.76	7	%N	Mauchline and Gordon (1984c)
	Group mean	3.71			
<b>Holocephalans</b>					
<i>Chimaeriformes</i>					
Chimaeridae	<i>Chimaera monstrosa</i>	3.46	56	%N	Mauchline and Gordon (1983)
	<i>Hydrolagus mirabilis</i> (25–47 cm)	3.47	21	%N	Mauchline and Gordon (1983)
	<i>H. mirabilis</i> (47.1–80 cm)	3.47	4	%N	Mauchline and Gordon (1983)
Rhinochimaeridae	<i>Harriotta raleighana</i>	3.40	8	%N	Mauchline and Gordon (1983)
	Group mean	3.44			

(2007). We calculated TLs for four species of holocephalans, and for members of six families of bathyal/abyssal teleosts following the methods of Cortes (1999), using his prey categories and TL values of prey items (Table 1). The proportion of each prey item ( $P_j$ ) in each species' diet was calculated according to Cortes (1999) using Eq. (1)

$$P_j = \frac{\sum_{i=1}^n P_{ij}N_i}{\left( \sum_{j=1}^{11} \sum_{i=1}^n P_{ij}N_i \right)} \quad (1)$$

where  $P_{ij}$  represents the proportion of prey category  $j$  in study  $i$ ,  $N_i$  represents the number of stomachs with food used to calculate  $P_{ij}$  in study  $i$ ,  $n$  is the number of studies used for calculating TL,  $j$  is the number of prey categories (Table 1), and  $\sum P_j=1$ . Following Cortes (1999) we calculated trophic levels with Eq. (2):

$$TL_a = 1 + \left( \sum_{j=1}^n P_j TL_j \right) \quad (2)$$

where  $TL_a$  is the trophic level of species  $a$ ,  $P_j$  is the proportion of prey category  $j$  in the diet,  $n$  is the total number of prey categories, and  $TL_j$  is the trophic level of prey category  $j$ .

We classified amphipods, isopods, copepods, mysids, euphausiids, or "other crustaceans" as zooplankton when calculating TL (Table 1). For studies ( $n=7$ ) that included a prey category of "unknown", this value was omitted and remaining prey categories were rescaled to compose 100% of the diet.

Following Cortes (1999) we used compound indices (e.g. index of relative importance, IRI) when available to apportion prey categories. Otherwise, single indices (percent frequency of occurrence, %F; percent number, %N; percent weight, %W; or percent volume, %V) were used individually. When two single indices were available, an average was calculated (e.g. (%F+%W)/2). The index

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